TAXONOMY AND OPERCULAR FUNCTION OF THE JURASSIC ALGA *STICHOPORELLA*

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ABSTRACT. *Stichoporella stutterdi* (Carruthers) Edwards is shown to differ from *S. cylindrica* (Lignier) Pia in the form of the distinctive opercula which terminated the side-branches in the reproductive stage of development; previous accounts of the difference were based on damaged examples. The opercula of *S. stutterdi* support the suggestion of Fily and Rioult (1976) based on *S. cylindrica*, as to their being formed immediately prior to cyst formation, and being shed to allow cyst-dispersal. The microstructure of the opercula in *S. stutterdi* is described. *S. cylindrica* is recorded only from the Middle Jurassic of northern France; *S. stutterdi* has a more northerly area of occurrence, overlapping with *S. cylindrica* in France but also occurring in the English midlands.

STICHOPORELLA is a large distinctive dasycladacean alga, occurring uncommonly in the Middle Jurassic of northern France and rarely in England. The genus was created for *Goniolina cylindrica* Lignier from the French Bathonian by J. Pia, who showed that this species was different in structural plan from a true *Goniolina* (Lignier 1913; Pia 1923, p. 68). Later Edwards (1928) recognized that a problematic English fossil earlier regarded as coral or crinoid, and described as a higher plant (*Aroides stutterdi* Carruthers), is in fact a second species of *Stichoporella*.

More recently Fily and Rioult (1976) have made a careful and very detailed revision of *Stichoporella cylindrica*, based on a new specimen of this rare dasycladacean. Rioult's emended generic diagnosis (op. cit., p. 40) may be translated as 'thallus cylindrical, not articulated, of large size, 15–16-mm diameter, with large axial cavity without constrictions or swellings. Alternate euspondyl verticils of phloiophore-type primary branches. At the exterior of the calcified cylinder, each pore (branch-termination) is closed by a laminated cupuliform operculum, free of the (calcified) cylinder and presumed deciduous, and closely inserted in the hexagonal areas (pores) which are delimited by the (honeycomb) ridges of the cylinder. All the branches could have been "fertile ampoules" (cladospore reproductive structures)' (see text-fig. 1).

Apart from its large size and very simple structure (many other Jurassic dasycladaceans are much more elaborate), *Stichoporella* is unusual in its distinctive branch-opercula, to which Fily and Rioult rightly draw attention, and largely because of which they place *Stichoporella* in a new diplopore tribe, the Stichoporellinae (Fily and Rioult 1976, p. 40).

Both Edwards and Fily and Rioult indicate that the only significant difference between *S. cylindrica* and *S. stutterdi* lies in the form of these opercula, the two species otherwise being closely similar in structure, proportions, and size. Edwards (1928, p. 80) wrote, 'It [*S. stutterdi*] differs from *S. cylindrica* in the dentate and dovetailing margins of the calcified membranes.' Fily and Rioult (1976, p. 40) wrote that *S. cylindrica* apparently differs only from *S. stutterdi* by the absence of denticules at the inter-

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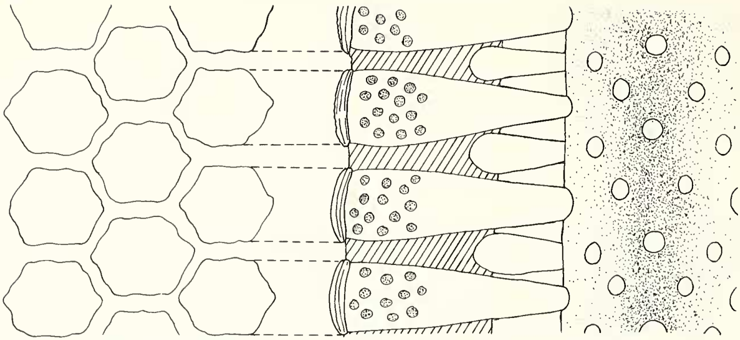

TEXT-FIG. 1. *Stichoporella*; diagram of structure. Left: surface pattern of opercula. Centre: radial swollen branches, terminating in opercula, cysts in outer parts of branches, calcification shaded. Right: axial or stem-cell cavity, to show initiation of branch-verticils.

section of the surface ridges delimiting the opercula. Their figure (op. cit., pl. 1, fig. 2) clearly shows the smoothly rounded hexagonal outlines of these opercula.

An attempt by me to evaluate this character in *S. stutterdi* and so determine the validity of the two species, led to the results set out below.

THE FORM OF THE OPERCULUM IN *S. STUTTERDI*

The English material is very limited, and comes from two localities only: Stonesfield in Oxfordshire (Bathonian) and Wittering, formerly in Huntingdonshire but now Cambridgeshire (Bajocian). Both are localities long since disused and overgrown; the fossils are from old collections. Stonesfield is the type-locality for the species, and the material from there is best preserved.

The cylindrical algae occur more or less compressed, to show a pavement of the opercula (Pl. 45, fig. 3). Most of these are represented by the underlying mould only,

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EXPLANATION OF PLATE 45

Figs. 1–4. *Stichoporella stutterdi* (Carruthers) Edwards; Stonesfield Beds, Middle Jurassic (Lower Bathonian); Stonesfield, Oxfordshire, England. 1. Single operculum, showing hexagonal-stellate outline, and gentle convexities and concavities on lower smooth well-preserved portion, ×20. Reg. no. V.10968. 2. Group of four opercula, showing characteristic flaked weathering which influenced earlier descriptions, ×20. Reg. no. V.5585. 3. Surface view of part of curved 'pavement' of opercula of this cylindrical fossil, ×8. Reg. no. V.10968. 4. Near-vertical thin-section of operculum, ×80. Left: edge of section; right: matrix (black and white). The section between shows the finely layered nature of the component calcareous lamellae: between these are developments of small calcite crystals, extensive on the left, minor on the right. Reg. no. V.5585a. Registration numbers above are those of the British Museum (Natural History), Department of Palaeontology.

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which can be recrystallized to a varying degree. Where the actual laminated operculum is preserved, it has usually flaked or scaled away to a varying extent. Careful search reveals the occasional near-perfect example. It is then seen that these are rounded and hexagonal to stellate in outline, with a porcellanous or enamelled surface appearance. From the flattened very slightly convex centre of each, alternate convexities and concavities in the outer slopes cause the stellate outline (Pl. 45, fig. 1), much as in certain brachiopods, e.g. *Zeilleria* (*Z.*) *quadrifida* (Lmk). There is a tendency during early weathering for the lamellar operculum to flake away differentially on the slopes of the convexities, so giving a spiky stellate outline (Pl. 45, fig. 2), and this is the origin of earlier statements on the 'dentate' outline and its interlocking properties. This is not so; the unweathered opercula are separated by the sinuous course of the terminations of the underlying calcareous coatings of the branches (the skeletal honeycomb structure). Whilst normally concavity is opposed to convexity in adjacent opercula, two opposed concavities sometimes occasion widening of the interopercular skeleton. Each rounded hexagonal-stellate operculum fits its own branch-termination ('honeycomb cell') and seems to have rested in the aperture.

S. stutterdi then, does differ consistently from *S. cylindrica* in operculum-outline, if not quite as previously described, and the character is accentuated by weathering. The Bajocian example available is very coarsely recrystallized, but the stellate outline is still recognizable. How significant is this one difference between the two described species? This is now considered in the light of the assumed function of the operculum.

STRUCTURE AND SIGNIFICANCE OF THE OPERCULUM IN *STICHOPORELLA*

Fily and Rioult (1976) have drawn attention to the markedly lamellar nature of the operculum in *S. cylindrica*, like a laminated watch-glass, and to the fact that this dense white structure has been preserved differently from the main skeletal calcium carbonate. They suppose the opercular flaking to be assisted by original interlamellar films of organic matter within the operculum (and record a negative test for aragonite, and the absence of silicification in this white calcareous structure). The opercula are said to rest in the rounded-hexagonal branch apertures on narrow rims. They are considered by these authors to be a special device behind which the reproductive cysts developed, and which were shed when the latter were released.

In thin-section the calcareous material of the operculum of *S. stutterdi* (Pl. 45, fig. 4) is seen to be finely layered and transparent within the different component lamellae. These are separated by planes of parting along which strings of small calcite crystals have developed during diagenesis. In contrast, the wall-material of the cylindrical skeleton is of uniformly coarse calcite crystals, representing the results of diagenesis on the original aragonitic skeleton, assumed by analogy both with living and with little-altered fossil dasycladaceans. This confirms an original difference in the composition of the operculum.

LIFE HISTORY

In living dasycladaceans the early growth-stages are not calcified. Only during later stages of growth does calcification develop to the usual extent for the particular taxon; it is especially liable to develop around reproductive structures when these individualize. This stage follows in the mature plant, on the break-up of the large nucleus in the rhizoid and the swarming of daughter nuclei into the stem-cell and branches, to originate the reproductive elements. These are contained in 'fertile ampoules' of varying form, usually filled with cysts but sometimes shedding free gametes direct, as in *Dasycladus* itself. Valet (1969) gives a detailed account of the various sexual and reproductive mechanisms in living Dasycladales. Fily and Rioult (1976) suggest that the outer swollen ends of the primary branches in *S. cylindrica* functioned as fertile ampoules, with the opercula as special containing devices.

If this was so, I would reconstruct the life-history of *S. stutterdi* as follows. It was an inhabitant of sheltered shallow coastal marine waters, as evidenced by the other fossils at Stonesfield and, when mature, was a thick-stemmed, thick-branched green alga, which eventually laid down aragonite in the mucilage between and coating the branches, to give the outer cylindrical honeycomb skeleton. At the end of its short life-span, probably one or at most two years, swarming of small nuclei up the stem-cell and into the terminal portions of the side-branches initiated copious cyst-formation. Hitherto, the rounded branch-tips had protruded beyond the skeletal mesh, with an assimilatory function. On the cessation of vegetative growth, they shrank. Against them, inside, from the biochemically changed cytoplasm of the reproductive period, there was laid down intermittently lamellar calcareous matter. I suggest this could have been calcium carbonate mixed with calcium oxalate, as is known from the reproductive discs of living *Acetabularia*. Whatever it was, it behaved differently during subsequent diagenesis to the granular skeletal aragonitic calcium carbonate. If this is what happened, the outer lamella of each operculum was the earliest formed. Subsequently, with cyst-ripening, the opercula were shed, the cysts dispersed, and the individual alga died or was perhaps regenerated from the shrunken rhizoid. Those now preserved as fossils were a minority, for some reason buried just before completion of the cycle.

If this hypothesis is true, why did the branches of *S. cylindrica* and *S. stutterdi* shrink differently, so occasioning the specific difference? Both species are recorded as occurring in France, around the Paris Basin (Dutertre 1926*a*, *b*, Gardet 1952, Fischer 1969, Fily and Rioult 1976), but *S. stutterdi* also occurs further to the north, in the English midlands. Were the two species perhaps ecophenes responding to differences in the marine climate? I have suggested (Elliott 1977) that *Stichoporella* was characteristic of a narrow climatic belt north of a Jurassic isocryme of major algal significance; this could perhaps be significant. However, as fossils they are morphologically distinct, and I confirm them as separate palaeontological species.

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